

The Choana, Maxillae, Premaxillae and Anterior Palatal Bones of Early Dipnoans

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The attempt by Rosen *et al.* (1981) to demonstrate the presence of a choana in dipnoans revolved around the identification of the bones forming the rostrum and the anterior end of the palate of *Griphognathus whitei* as homologues of the vomers, palatines, maxillae and premaxillae of tetrapods. These homologues were postulated on the basis of similar patterns of bones in the two groups. Studies of the function of the bones in question and of their evolution from the primitive dipnoan condition, have shown that these conclusions cannot be sustained. *Griphognathus whitei* is a highly derived species with neomorphic bones formed in response to an unusual mode of feeding. The rostral ossification is formed by the fusion of bones after the dipnoans separated from their parent group, and it does not contain homologues of the premaxillae. In this instance, the attempt to establish relationship by outgroup comparisons without an analysis of the ingroup relationships in evolutionary and functional terms, is inappropriate. Studies of pattern and process must proceed hand in hand.

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INTRODUCTION

Dipnoans have either lost or never had marginal tooth rows. Since they appeared in the fossil record in the Early Devonian, they have had palatal and prearticular teeth which have displayed a variety of grossly different patterns and functions (Campbell and Barwick, 1983). Recently, several attempts have been made to interpret the nature of the dentition in primitive lungfishes. This is a matter of some importance, as the recent work of Rosen *et al.* (1981) has raised again the issue of the relation between the Dipnoi and the Amphibia, suggesting that they are sister groups. Implicit in that hypothesis is the view that marginal tooth rows were present in the ancestors of the Dipnoi, and persisted in that group at least during its early evolutionary phase, becoming modified as palatal teeth became more effective.

It was the supposed identification of the choana in the Late Devonian dipnoan *Griphognathus whitei* that suggested to Rosen *et al.* the need to reinvestigate dipnoan/tetrapod relationships. In that species, the identification of the choana is dependent on the recognition of the homologues of its surrounding bones, a point that is made clear in their introduction to the topic (Rosen *et al.*, 1981: 178-182). The choana in early tetrapods, exemplified by *Ichthyostega*, is surrounded by the vomer, the palatine and the maxilla, and these three bones were said to be recognized in *G. whitei*. The homologues proposed by Miles (1977) were abandoned. In our view, their case depends on special pleading, takes no account of variation in the number and the position of the bones present, ignores the fact that this species shows many derived characters quite unknown in earlier dipnoans, and makes no attempt to understand the structures concerned in functional terms.

In the ensuing discussion the arrangement of the bones in question will be described for *G. whitei*, their positions in other primitive dipnoan species will be

discussed, an attempt will be made to interpret the structure of *G. whitei* in functional terms, the homologies of the bones will be outlined, and as a consequence it will be shown that no evidence supporting the presence of a choana in the Dipnoi can be derived from *G. whitei*. This being so, the case for the dipnoan/tetrapod relationship proposed by Rosen *et al.* is considerably weakened.

For discussion purposes, the bone names used by Miles (1977) and Rosen *et al.* (1981) are employed, but they are placed in quotation marks to indicate that we question their validity.

BONES AROUND THE ANTERIOR END OF PALATE OF *GRIPHOGNATHUS WHITEI*
'Dermopalatines 1 and 2' or 'Vomers'

At the anterior end of the palate is a pair of bones ('dermopalatine 1' of Miles, 1977, and 'vomer' of Rosen *et al.*, 1981), which can be recognized in all specimens examined to date. They continue the contours of the pterygoids. In some specimens, an elongate element ('dermopalatine 2' of Miles, and 'palatine' of Rosen *et al.*), which moulds itself around the inner margin of the posterior naris, lies posterior to the 'dermopalatine 1'. It separates the posterior nostril from the pterygoid in the specimen considered to be typical by the above authors. As Miles (1977: 163) indicated, this bone is not invariably present, and where it is present it varies considerably in length. In some specimens the same space is occupied by the expanded pterygoid, and in others a single dermopalatine (or vomer) flanks the pterygoid between the mid-line and the posterior naris (see Fig. 2A-C). It is necessary to justify the assumption that

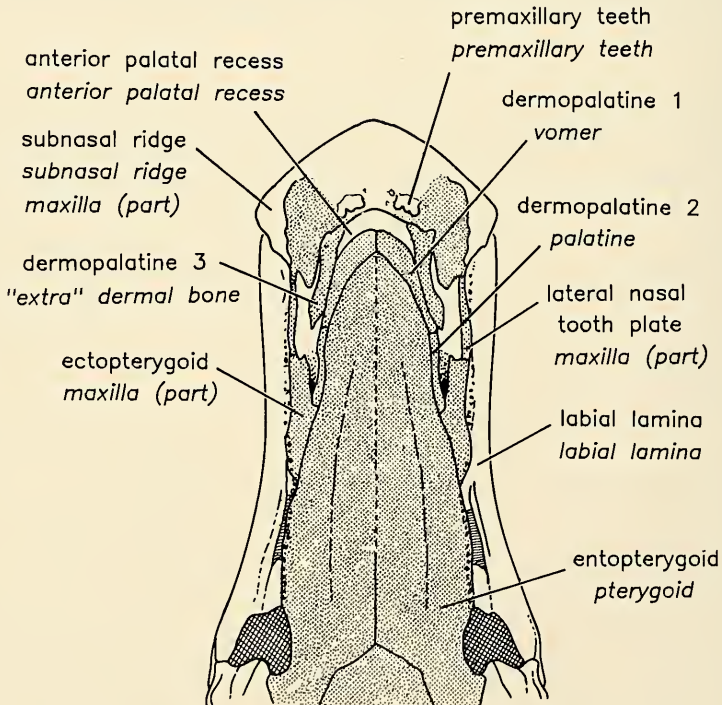


Fig. 1. Anterior part of the palate of *Griphognathus whitei* copied from Miles, 1977: fig. 6, and labelled with his bone identifications and those of Rosen *et al.*, 1981. The upper label (upright letters) is from Miles, and the lower label (italics) is from Rosen *et al.* Note that we consider the presence of dermopalatines 1 and 2 to be abnormal.

'dermopalatines 1 and 2' are typical of *G. whitei* and that this represents the primitive condition.

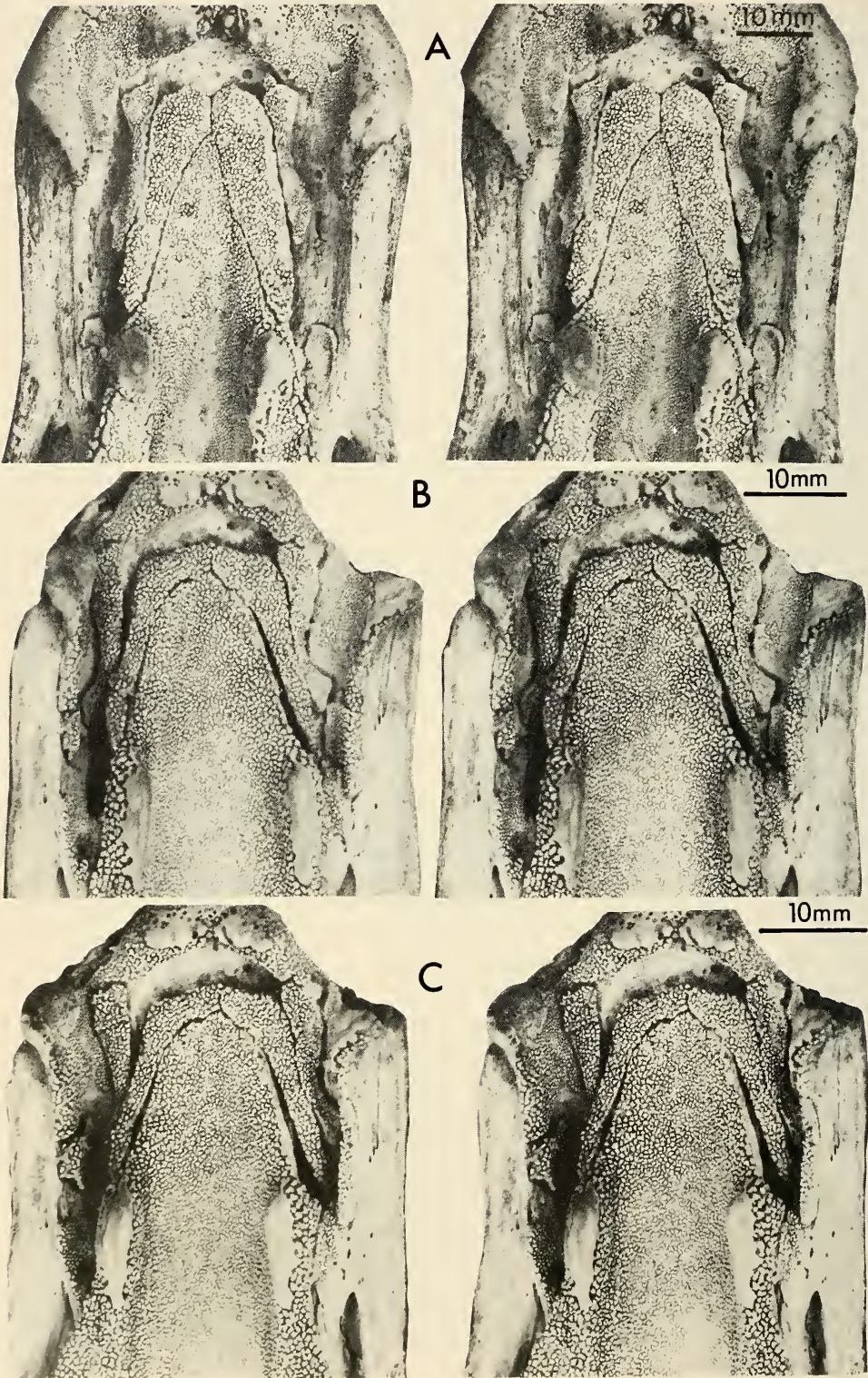
In the primitive genera *Uranolophus* (Denison, 1968), *Dipnorhynchus* and *Speonesydrion* (Campbell and Barwick, 1983) a single bone occupies the space on each side anterolateral to the pterygoid between the mid-line and the postnasal wall. The position in *Fleurantia denticulata*, in which Graham-Smith and Westoll (1937) have restored a single dermopalatine, is not clear. Because a single bone occupies the same space in several specimens of *G. whitei*, and a similar situation occurs in *G. sculpta* (Schultze, 1969: fig. 14), it is reasonable to conclude that this is the typical condition in *Griphognathus*. The second bone (i.e. the one labelled 'dermopalatine 2' by Miles and palatine by Rosen *et al.*) is an individual variation within *G. whitei* and is of no significance in determining homologies. Its presence is functionally related to the great increase in the distance between the postnasal wall and the anterior end of the palate. The occurrence of a single bone in all other Devonian genera indicates that this is the primitive condition and the use of the specimen of *G. whitei* with two 'dermopalatines' as typical of the primitive condition is unjustified.

For present purposes the homology of the single bone between the midline and the post-nasal wall is not a matter of consequence, except in so far as it has quite the wrong relationships to be a palatine, a point to which we return later.
'Ectopterygoid' or 'Maxilla'

The bone immediately posterior to the 'dermopalatine' has similar characteristics, but it does not form part of the arcade continuing the palatal contours. Instead, its inner edge stands up abruptly from the pterygoid and then moulds itself to the ventral surface of the postnasal bar. This latter structure is well ossified in all Devonian dipnoans, and runs laterally to form a broadly expanding buttress against the inner surface of the roofing bone that contains the anterior part of the suborbital lateral line (Fig. 2A-C). The bone in question, which is interpreted as the 'ectopterygoid' by Miles (1977: fig. 57), and as part of the 'maxilla' by Rosen *et al.* (1981: 185, fig. 7A), is very thin, denticulated, and appressed to the surface of the postnasal bar. Laterally it is sutured against the concave and sharply defined labial lamina which is discussed below. It lies around the lateral and posterior edges of the posterior naris. Miles (1977: 180) gave a good account of the bone and its relationships. There is no doubt that it lies on the lateral face of the tectum nasi (above which lie the ramifying sensory tubules of the snout) as well as on the postnasal bar. Its outer edge, on which the denticles are slightly enlarged, is aligned with the outer edge of the lateral nasal tooth plates. It is clearly sutured against the ridge labelled 'endoskeletal ridge supporting tooth-ridge' by Miles (1977: fig. 78), as is shown on Fig. 2A, B.

'Lateral Nasal Tooth Plates' or 'Maxillae'

The anterior edge of the bone designated as maxilla by Rosen *et al.* (1981: fig. 7a) is not clear. In at least some of our specimens it is a short bone, and this is probably the norm. In ANU35641 one, or possibly two lateral nasal plates (Miles, 1977: 181) lie between its anterior edge and the subnasal ridge (Fig. 2B, C). These lateral nasal tooth plates consist of an almost horizontal outer, lateral sector, and a vertical inner sector that turns inwards slightly along its dorsal edge, partly to join with the 'dermopalatine 3' of Miles (see below), and partly to form the lateral margin of the anterior naris. They broadly follow the contours of the ventral surface of the tectum nasi. More than one lateral nasal tooth plate may be present, as was indicated by Miles (1977: 181), but it is difficult to distinguish between cracks and sutures on most specimens. The anterior edges of the lateral tooth plates are generally clear, though they vary slightly in position from specimen to specimen. Their contours continue smoothly into the concave ventral face of the rostral capsule.



It is of importance to establish that these tooth plates are sutured against endocranial bone, and that the sutures frequently open allowing them to fall free. Some confusion may arise from the identification by Miles (1977:180, fig. 78) of a separate entity named the labial lamina, which he characterized as 'an internal lamina of anterior bones in the infraorbital lateral-line series'. This lamina is said to lie against an endoskeletal ridge that supports the ventral edge of the lateral nasal tooth plates. The edges of the external dermal bones (probably 1a-c) are not inflected along this edge. Topographical relations and thin sections both show that the endocranium is deflected outwards to meet the external bones to form the main lamina (Fig. 3). The boundary between the endocranium and the dermal bones is difficult to distinguish clearly in the sections, but it is clear that the lamina as well as the ridge supporting the lateral nasal tooth plates is of endocranial origin. The tooth plates are not in contact with the external dermal bones 1a-c.

Such an arrangement is possible in *G. whitei* only because the dermal bones 1a-c are so elongated and the snout is so depressed. Species such as *Chirodipterus australis* have the postnasal bar standing up much more steeply so that it makes contact with bones 1a-c only along their dorsal edges (Figs 4A, 5B).
'Dermopalatine 3' or 'Extra Dermal Bone'

One other loosely articulated bone is present in this region in all specimens examined. It is labelled 'dermopalatine 3' by Miles, and as an 'extra dermal bone' by Rosen *et al.* (1981: fig. 7A). In both ventral and lateral aspects this bone is always strongly flexed. Its lateral edge forms the margin of the anterior naris, which must have been directed anteriorly from the nasal capsule. Its posterolateral edge was probably loosely articulated with the inner edge of the lateral nasal tooth plate, thus forming a continuous but flexible roof over the entrance space to the anterior naris. As Miles (1977: fig. 80a) has shown, this flexible junction is sometimes lost by fusion of the adjacent bones. In some specimens (BM P56054 and ANU35641), the 'dermopalatine 3' articulates with the posterior denticulated edge of the rostral capsule, but in others there is a gap at its anterior edge. This gap may have been occupied in life by yet another denticulated plate.

No equivalent of 'dermopalatine 3' is known from any other dipnoan. One may have been present in other long-headed forms such as *Fleurantia* or *Soederberghia*, but further material is needed. No short-headed species shows evidence of such a bone. Indeed, one would not be expected, because the anterior naris in such forms is situated well forward, immediately behind the edge of the notch in the rim of the rostral capsule. A similar argument would apply to *Uranolophus wyomingensis* in which the posterior edge of the notch for the anterior naris is sharply defined and stands up to form a steep non-denticulated rim.

Miles and Rosen *et al.* have been unable to homologize this bone with bones in osteichthyans or amphibians. The conclusion that it is neomorphic seems inescapable.
'Vomer' — A Median Unpaired Plate

Was a median unpaired bone present at the front of the palate of *G. whitei*? Miles (1977: 165) found the possibility of such a bone attractive because it 'would occupy the same morphological position as the vomer in *Chirodipterus* and *Holodipterus*'. He found no bone *in situ* in this position in his material, and we have found none in ours. One median non-denticulated bone (Miles, 1977: fig. 83) was treated as a possible candidate, but neither its shape nor its structure support this identification. Moreover, *G.*

Fig. 2. Views of the anterior part of the palates of two specimens of *Griphognathus whitei* showing the arrangement of the various denticulated structures. A and C are full ventral views of CPC22593 and ANU35641 respectively. B is of ANU35641 tilted slightly to the right. Scale = 10 mm.

whitei normally has neurocranial shelves to support the loose bones such as 'dermopalatine 1' and 'dermopalatine 3', but no shelf is present to support a median dermal bone. We consider that no such bone was present.

The only Devonian species for which unequivocal evidence of a median anterior unpaired bone exists is *Chirodipterus australis*. *Scaumenacia curta* as figured by Jarvik

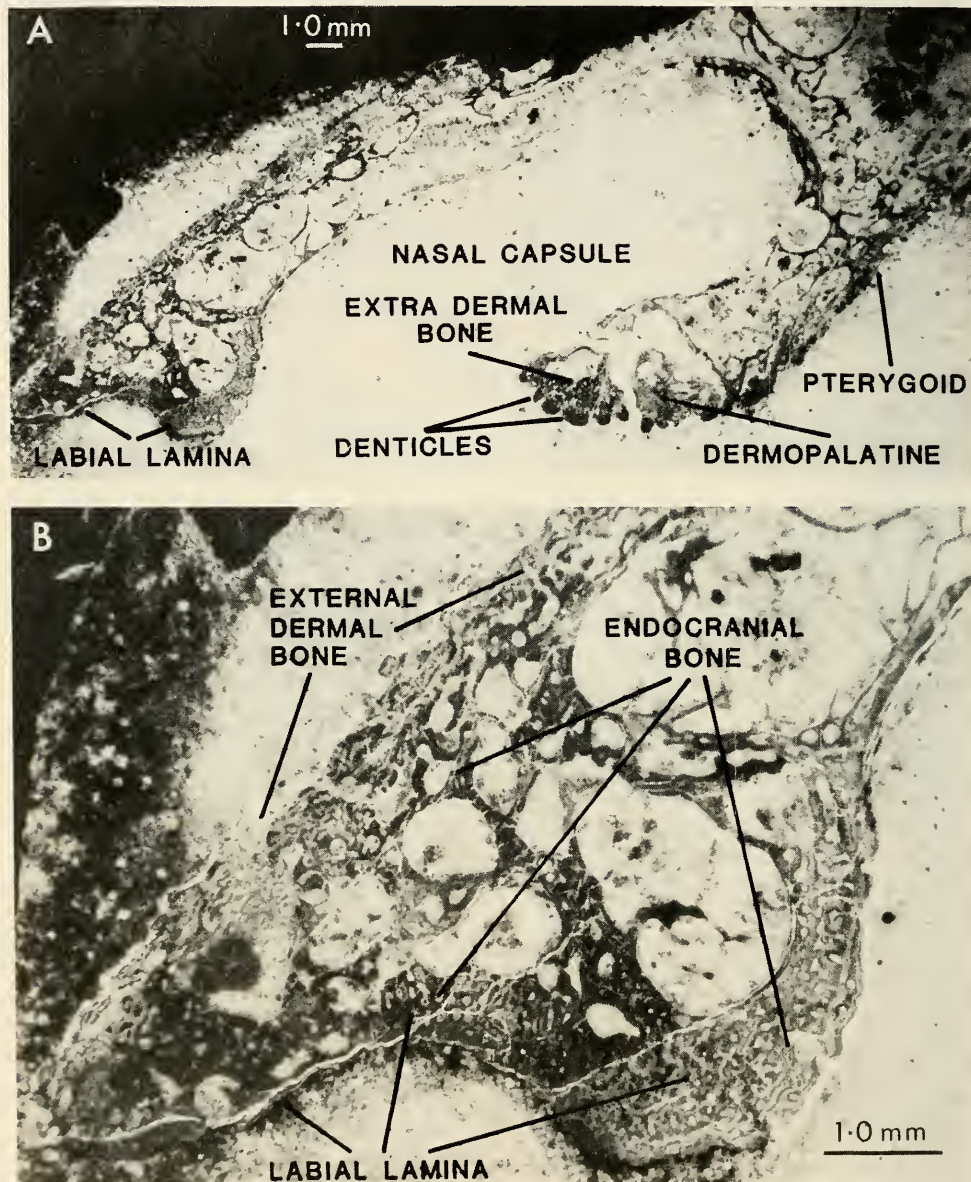


Fig. 3. Cross section of the nasal capsule of *Griphognathus whitei*. A. General form of the endocranial bone, lining the capsule; the denticle-bearing 'dermopalatine' and 'extra dermal bones' lying against the 'pterygoid' and the external dermal bones and labial lamina, the latter without the 'lateral nasal tooth plates' covering its inner surface. B. Enlargement of the labial lamina which is formed entirely of endocranial bone without an inflected cover of external dermal bone. Dark field illumination.

(1967: pl. 6, fig. 5) is said to show a bone of this type. Examination of the specimen has left one of us (KSWC) unconvinced. In addition to the specimens of *C. australis* mentioned by Miles, ANU35638 shows the median unpaired bone admirably (Fig. 5). None of the specimens of *C. australis* have the 'dermopalatines 1' meeting in the mid-line as they do in all three Early Devonian genera *Uranolophus*, *Dipnorhynchus* and *Speonesydrium*. Miles expressed the view that the 'dermopalatines 1' primitively met in the mid-line and paired bones (the vomers) lay in front of them. According to this view the 'dermopalatines 1' in *Chirodipterus* have become smaller and withdrawn from the mid-line, leaving a median space into which the now fused vomers have moved. Miles (1977: 175) has argued that the vomer 'is primitively paired in choanates, actinistians and actinopterygians', and that paired vomers are known in all the recent dipnoan genera as well as the late Palaeozoic *Sagenodus*, *Uronemus*, *Conchopoma* and *Monongahela*. Unfortunately no reason is given for homologizing the paired bones in these genera with the median unpaired bone in *Chirodipterus* (the 'vomer') rather than the paired lateral bones (the 'dermopalatines 1'), an hypothesis that seems to us to be at least equally probable. The outgroup comparison argument is irrelevant for purposes of determining whether these bones are the homologues of the 'dermopalatines' or the median unpaired 'vomer'. We conclude that no case has been made in support of the view that paired bones or an unpaired bone lay in front of the 'dermopalatines 1' in *Griphognathus whitei*.

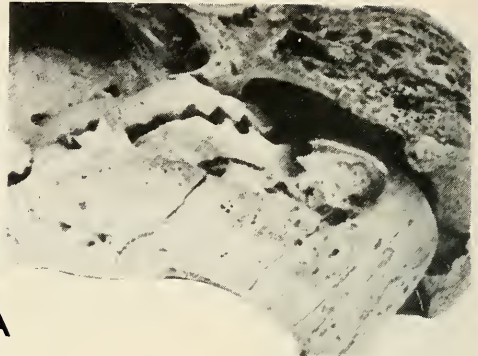
The Rostral Ossification

The denticulated parts of the rostral ossification remain to be discussed. This is a massive structure, largely covered by a sheeting of dentine and enamel (Smith, 1977: 33) that breaks down into denticles in the region of the notches leading to the anterior nares. Unlike most Devonian dipnoans, this structure has an extensive ventral surface produced from backwardly deflected external bone that forms a ventral cover for the anterior part of the ethmoid capsule. The lateral part of this cover, which forms the subnasal ridge of Miles (1977), lies well behind the anterior edge of the palate. This relationship is possible only because of the attenuation of the snout in *Griphognathus whitei*. It is quite impossible in shorter-headed forms, be they of the tooth-plated type like *Chirodipterus* or the non-tooth-plated type like *Holodipterus*.

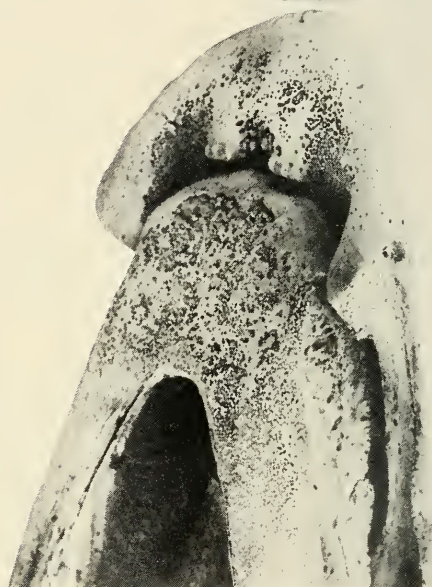
No sutures are present on this surface, but topographically it is divided into three elements — a pair of pre-oral eminences, very prominent subnasal ridges, and very broad anterior narial notches. The pre-oral eminences usually carry a few coarse tubercles on their crests and smaller denticles on their lateral and posterior faces. The notches are broadly rounded and lined with a thin layer of denticulated dermal bone that extends posteriorly a considerable distance to meet the edge of 'dermopalatine 3', and then runs lateral to that bone until it meets the lateral nasal tooth plates. This surface continues laterally in a smooth curve up the inner face of the subnasal ridge.

Rosen *et al.* (1981: 180-181) refer to the tubercles on the pre-oral eminences as 'premaxillary teeth', and they believe that these eminences 'represent premaxillae that have fused with the bone of the snout'. It is not clear where these supposed 'premaxillae' and the 'bone of the snout' join. They also regard the slightly enlarged denticles that occur on the subnasal ridge in some specimens as 'maxillary teeth'. As has been shown above, the subnasal ridge is quite separate from the more posteriorly placed lateral nasal tooth plates, which they also regard as 'maxillary', but this ridge cannot be separated from the remainder of the rostral ossification which is not part of the 'maxillary'.

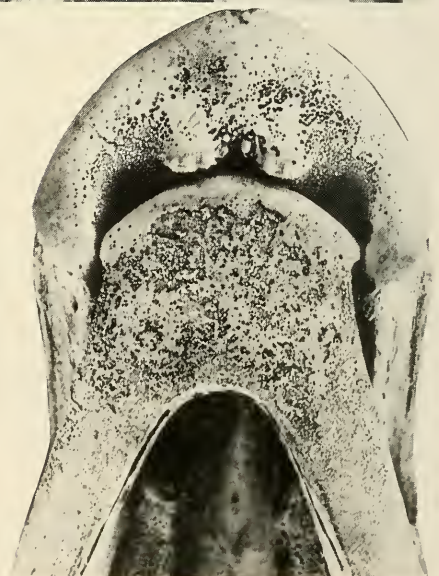
Interpretation of these bones should be made in terms of what is known about the rostral region of other Devonian dipnoans rather than by outgroup comparison. When that is done, a completely different picture emerges, as is shown below.



A



B



C

THE ANTERIOR AND POSTERIOR NASAL OPENINGS IN *G. WHITEI*

As was clearly shown by Miles (1977: fig. 57), the nasal capsules are relatively small and lie more posteriorly than in most other species. They are also more protected on the ventral side by the pterygoids than in any short-headed dipnoan known to us. The anterior opening for the nasal capsule must have been situated in the notch in the 'dermopalatine 1', and it must have entered the capsule from a slightly anterolateral direction. It would have had a depressed oval outline, and it must have been in a more posterior position than that indicated by Miles (1977: fig. 57). The posterior naris was in the position indicated in that figure, but its shape cannot be defined from the material at our disposal. The bone edges around the space for this naris are not always 'finished', and presumably the actual opening was in loose skin.

The anterior naris was therefore well behind the anterior nasal notch in the rostral capsule, quite unlike the situation in any known short-headed dipnoan with tooth plates. Forms such as *Dipnorhynchus* and *Chirodipterus* (Fig. 8) have large nasal capsules situated anterior to the dentition, and the anterior naris was placed immediately posterior to the anterior nasal notch. Similar comments seem to be applicable to *Uranolophus*, which is the most primitive of all the denticulated types, though in *U. wyomingensis* the capsule details are not completely clear. However, even the relatively short-headed denticulated types such as *Holodipterus* have much smaller nasal capsules that are partly covered by the pterygoids and adjacent denticulated plates, and the anterior naris must be situated well back from the anterior nasal notch which is itself denticulated.

The posterior naris in *G. whitei* was in a very posterior position relative to the front of the palate. It was tucked into the angle formed at the junction of the postnasal wall and the pterygoid. With a similarly small nasal capsule, the posterior naris of *Holodipterus* must also have occupied a posterior position. On the other hand, the posterior naris in *Dipnorhynchus* and *Chirodipterus* would have been further forward, being about half way along the length of the 'dermopalatine 1' (see Thomson and Campbell, 1971: fig. 29; Miles, 1977: fig. 67).

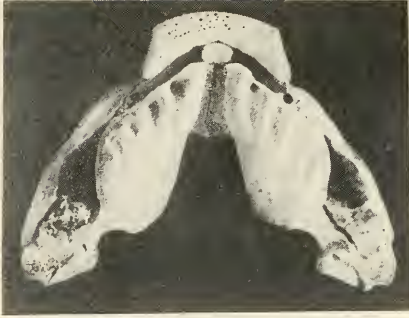
OCCLUSION IN *G. WHITEI*

The arrangement of the bones around the nasal capsules in *G. whitei* can be understood only if the occlusal pattern of the jaws is appreciated. Other long-headed dipnoans may share a similar pattern, but the only genus for which the specimens are sufficiently well preserved for this to be established unequivocally is *Griphognathus*. Several undistorted specimens of *G. whitei* have been found with the mandible preserved in position. These illustrate a number of points:

1. The largest 'prearticular' tusk passes lateral to the large pterygoidal tusk, and meets the ventral face of the postnasal bar. On some specimens, this bar has a distinct pit to receive the crest of the 'prearticular' tusk. Clearly the denticulated dermal bone (maxilla of Rosen *et al.*) on the surface of the postnasal bar served as a protection during full occlusion and also assisted with the holding of food. Such a relation is not possible in other dipnoans.

2. The crest of the 'dentary' passes with a shearing action between the den-

Fig. 4. A. Ventrolateral view of a weathered specimen of *Chirodipterus australis* (ANU35640) with the lower jaw in position showing the relation of the tooth plates to the postnasal bar. *B, C.* Two views of a specimen of *Griphognathus whitei* (CPC22593; see also Fig. 2A) showing the extent to which the lower jaw occludes the anterior nasal notches and the space along the inner edge of the labial lamina. Note that the lateral nasal tooth plates are missing, leaving a larger slit than would have occurred in life. Compare this situation with that of *C. australis* shown in Fig. 5C. Natural size.



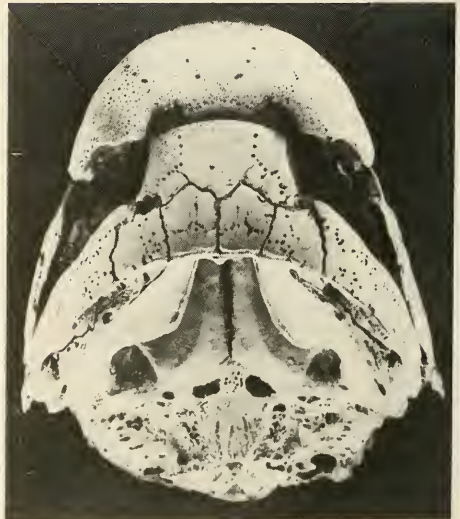
A



B



C



ticulated surface of the subnasal ridge and the lateral nasal tooth plates on its outer side, and the 'dermopalatines' on its inner side. Its crest then fits neatly into a groove that is roofed in part by the anterior palatal recess, the backwardly deflected bone of the rostral capsule, 'dermopalatine 3', and the inflected edges of the lateral nasal tooth plates.

3. The anterior edge of the 'dentary' lies behind the preoral eminences of the rostral capsule, and does not even contact the denticles on the posterior surfaces of these eminences. Articulated specimens show that the fit of the lower jaw is so tight that it cannot be moved forwards to make such a contact. The relationship indicates either a grasping or a shearing action which is almost exactly the same as that between the lateral parts of the 'dentary' and the lateral nasal tooth plates. The only difference is in the increase in size of the denticles on the preoral eminence. This modification would be expected in the light of the fact that the mouth opening was restricted to the space between the subnasal ridges (see Campbell and Barwick, 1983: 41), and special grasping structures would be necessary in this position.

4. At full occlusion both the anterior and posterior nares are completely covered by the crest of the 'dentary'. A slight gap remains between the 'dentary' and the anterior end of 'dermopalatine 3', but this would have left a very narrow passage between the anterior nasal notch and the anterior naris (see Fig. 4B, C). The fit is so close that the nasal apparatus could not be fully functional when the mouth was closed.

The above-mentioned features may not be unique in *G. whitei*, but they certainly are not present in any of the short-headed types with or without tooth plates. Even in *Uranolophus* the bite did not bring the 'dentary' into close contact with the nasal capsule or the post-nasal bar, and hence in this genus as well as in such tooth-plated forms as *Chirodipterus*, denticulated plates to cover these structures were unnecessary. Any explanation of such bones in *G. whitei* has to take into account the fact that they are not primitive but derived to serve a function related to the distinctive bite of this genus. Further, this distinctive bite occludes both the anterior and posterior nasal openings more effectively than does the bite of any of the primitive forms.

FUNCTION OF THE POSTERIOR NASAL OPENING IN DIPNOANS

The emphasis elsewhere in this paper is on structure, but in this section we examine the functional significance of the position of the posterior nasal opening inside the mouth. In so doing we are partly constrained by what is known of the functions of the living dipnoan genera, by what can be inferred of the structure of the nasal organs of fossils from the shapes of their surrounding hard tissues, and by information on the environment in which the early genera evolved.

Dipnoans are now thought to have evolved in the sea, and it is clear that even the most primitive genera had nasal capsules similar in structure to subsequent forms that became adapted to life in freshwater streams and lakes. Therefore we cannot accept the view that the dipnoan nasal apparatus evolved in response to special conditions associated with the freshwater environment, such as relatively anoxygenic standing water bodies, or ephemeral streams in 'old red sandstone' environments.

All three living dipnoan genera gulp air through their mouths. None respire through their nasal capsules (see Atz, 1952, for summary). *Neoceratodus* lives in quiet

Fig. 5. A single specimen of *Chirodipterus australis* ANU35638. **A.** The isolated mandible showing the ad-symphysial plate that occludes with the anterior median plate of the palate shown in **B.** **C.** Whole specimen with the lower jaw in position and showing the relatively open anterior nasal notch and the large labial spaces which indicate that the passage of water through the nasal capsule was little affected by closure of the mouth. Natural size.

water bodies that are often poorly oxygenated. *Protopterus* and *Lepidosiren* live in lakes or rivers, and have a capacity to aestivate. All three apparently swim to the top of the water and gulp air as required. Primitive dipnoans in the sea may not have been able to do this. They were all heavily ossified bottom feeders. However, even if they were able to use their fins and hydrostatic structures to get to the surface it can be safely assumed that like living species they gulped air and the nasal apparatus took no part in respiration. Even assuming that the so-called marine species were catadromous, and that in the sea they depended on gill respiration but in rivers and lakes they were able to respire by gulping air, the argument that the mouth had to be open to take in air would still apply. Moreover, the body design of these fishes would not permit seasonal, migratory habits, so a catadromous mode of life can be ruled out. We know of no structural or environmental evidence to support the view that primitive genera had a nasal respiratory capacity that has since been lost.

A second possibility is that the opening served a dual function — passage of water for olfaction and water from some accessory structure such as a nasal aspirator. Aspirators are known in some living teleosts that are either sessile or slow moving, and require some additional means for producing a water flow through the nasal capsule (Atz, 1952). Early dipnoans give evidence of being slow moving, but it would be difficult to argue a case for an aspirator unless there was strong morphological support from the structure of the bony lining of the nasal capsules. Inferences can be made from structures preserved in *Dipnorhynchus* (Thomson and Campbell, 1971: fig. 29), *Griphognathus* and *Chirodipterus* (Miles, 1977: 135), but these are not sufficiently precise to support or contradict this hypothesis, which must therefore remain as a speculation. One further point that may argue against the presence of an accessory aspirator is that *G. whitei* has a very small capsule, much smaller than those of the other genera, and little space would have been available for such a structure. In fact, closure of the mouth would compress the capsules, and it may well be that by appropriate use of valves water could be forced through the capsules by this means. However, we see no evidence to support an argument for a dual function of the posterior nasal opening involving an accessory organ. This does not rule out the possibility of a dual use of the water but, so far as we can determine, no adequate proposal of this kind has been put forward. The suggestion of Atz (1952: 376), for example, that the internal position would allow respiratory water to be used to prevent desiccation of the lungs and gills can only be regarded as improbable in view of the fact that the animals evolved in the sea.

Consequently we are forced to the conclusion that the function of this opening is to allow passage of water for olfaction, which is not surprising in view of the fact that this is its only function in living species.

Having decided that the function is olfactory, it does not necessarily follow that the posterior nasal opening is a posterior naris that has migrated into the mouth. Such a view assumes (a) that the position of the posterior naris outside the mouth is primitive for osteichthyans and (b) that in dipnoans this opening is not a neomorphic structure serving the same function as the posterior naris in other osteichthyans. Miles (1977: 147) has reviewed the first point. We are in agreement with him and with the large number of workers he quotes, that the posterior naris is primitively outside the mouth. Acceptance of the view that the opening is neomorphic, but serves the same function as a posterior naris, would require strong independent support, and this has not been forthcoming.

Hence we are left with the hypothesis that in the Dipnoi the posterior naris has migrated into the mouth. This hypothesis was championed by Jarvik (1942), and has received support from many later workers (Bertmar, 1965; Panchen, 1967; Miles, 1977). It has been further developed by Jarvik (1980). Evidence favouring this view

rests largely on evolutionary functional morphology, but this does not depend on demonstrating a positive advantage for an internal opening. Rather it depends on showing that it is a concomitant of other adaptive changes characteristic of dipnoans.

Marginal to the mouth in the ancestors of the Dipnoi and other osteichthyans there must have been bones that had developed, or were in a position to develop, marginal teeth. It is not known if these bones were paired to form maxillae and premaxillae, or consisted of a greater number of smaller bones (but see Chang and Yu, 1984). The important point is that as dipnoans gained their distinctive palatal bite, these marginal bones atrophied. The row of suborbital lateral line bones, which were primitive in osteichthyans, thus came to border the mouth laterally. (A similar phenomenon seems to have occurred as early as the Devonian in the Actinistia, though this does not necessarily imply a close relationship between the two groups.) Anteriorly the situation is more complicated. However, assuming that the anterior marginal bones also atrophied, the anterior and posterior nares would have come into positions marginal to the mouth. Associated with this change, modification of the palatal bones must also have been taking place. The so-called 'prearticular' tooth plate was developing to meet the 'pterygoid' and 'dermopalatine' teeth, and these were concentrating to leave a marginal gap between themselves and the outer dermal marginal bones. This gap was skin covered. With further evolution the nares moved into this gap, and then assumed the standard dipnoan arrangement.

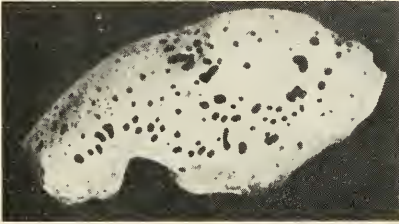
This view not only provides a functional interpretation of the movement of the nares, but it also accounts for the peculiarities of the lateral line system in the snout region of dipnoans so frequently commented on since Jarvik (1942) proposed that the incomplete infraorbital lateral line resulted from 'the fact that the lateral nasal wall with the fenestra endonarina communis and associated soft tissues and exoskeletal parts has been bent inwards below the nasal sac' (Jarvik, 1980: 393). If the lateral-line-bearing bones in the region of the nasal capsule were lost, the loss of the anterior end of the suborbital line and the ethmoid commissure would be neatly explained along with the fact that the supraorbital canal terminates anteriorly in a large pore. As has been shown by Campbell and Barwick (1982) the infraorbital canal in *Dipnorhynchus kiandrensis* passes inside the dermal bone in the snout and enters the mass of rostral tubuli. A recently-collected dipnorhynchid from Wee Jasper (see Fig 6B, C) shows a row of large pores around the anterior edge of the rostrum in a position approximating to the putative position of a continuation of the infraorbital canal, but these large pores all open into large rostral tubuli. The supraorbital canal, though maintaining its integrity, is also intimately connected with these tubuli.

These observations support the view of Westoll (in Lehmann and Westoll, 1952: 414) that the absence of the ethmoid commissure in dipnoans is secondary, but they do not support his general thesis. Rather, they suggest that the ancestors of the Dipnoi already had a system of rostral tubuli that functioned as seismosensory structures and were innervated by the profundus, ophthalmicus superficialis and buccalis lateralis nerves. When the ethmoid commissure was lost, the lateral line system, which in this region is innervated by the same nerves, became integrated with the tubuli.

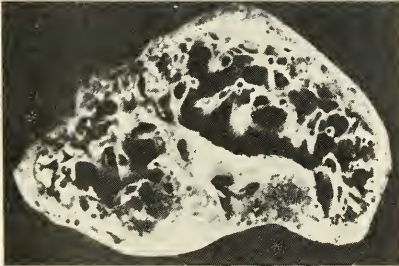
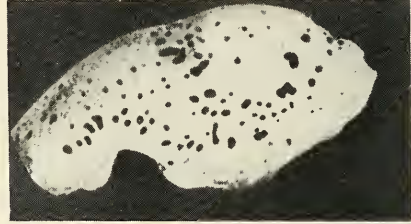
We note Westoll's comments (in Lehmann and Westoll, 1952: 418) that Jarvik in his argument that the nares have been turned into the roof of the mouth in dipnoans 'relies heavily on the course of the r. maxillaris V in *Epiceratodus*, internal to the ex-current posterior nostril; but its relations to the vomer are very abnormal. Moreover, in the same fish the r. buccalis lateralis runs *outside* the nasal sac and at least the posterior nostril; in all fishes known to the writer this never passes *ventrally* to the posterior external nostrils'. Neither of these objections carries much weight. As we will show below, the homology of the 'vomers' in the Dipnoi is open to question, and the



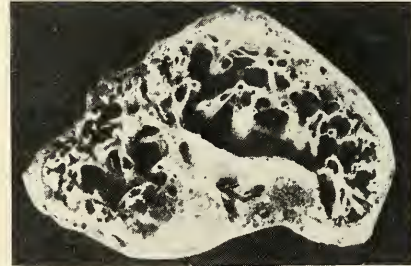
A



B



C



D



course of the buccalis lateralis nerve became modified in early dipnoans as its connection with the rostral tubuli probably developed after the loss of parts of the anterior lateral lines.

This provides a feasible morphological and functional interpretation of the bone pattern, the nares and the sensory systems of the rostral region. It requires no assumption of taxonomic relationships.

Set in opposition to arguments of this type are those of Rosen *et al.* (1981) who have attempted to establish without reference to function, evolutionary history or environment, that the posterior nasal opening in dipnoans is a choana. They have relied on the determination of bone homologies in *G. whitei*. We now turn to a discussion of this attempt.

HOMOLOGIES OF BONES AROUND THE ANTERIOR END OF THE PALATE IN DIPNOANS

The pattern of bones in this region varies considerably from genus to genus, and there is conflict of opinion on homologies *within* the Dipnoi. Authors usually state their conclusions without indicating what criteria have been used. The situation is further confused by the use of bone names defined for other groups, so that one is unsure if completely unlike bones in the Dipnoi (say the unpaired 'vomere' of *Chirodipterus* and the paired 'vomeres' of *Neoceratodus*) are homologized by comparison with non-dipnoan vomers, or by direct comparison with other dipnoans.

The logical approach to this problem is to argue a set of internally consistent homologies for the Dipnoi first, and then to examine the possibility of determining the relations between these and the bones of other groups.

Premaxilla

Miles (1977) and Rosen *et al.* (1981) assert that a premaxilla is present, the former author not attempting to set limits to the bone, and the latter authors restricting it to the dentigerous bone between the anterior nasal notches. As was shown above, there is no evidence to suggest the presence of paired bones in this region of *Griphognathus* (or any other described genus), and consequently argument in favour of homologies with other groups is rendered difficult, if not impossible. Rosen *et al.* (1981: 185) use morphological criteria to identify the premaxillae — 'they bite outside the lower jaw, they are the most anterior teeth in the upper jaw, and lie immediately in front of the anterior palatal recess . . .'. Elsewhere (pp.180-181) these authors add the criterion that they are 'in series with a more posterior upper jaw dentition (as are premaxillae with maxillae) . . .'. Miles (1977:186-187) offers a phylogenetic argument in support of his view — dipnoans are teleostomes that are collateral descendants of crossopterygians, and hence would be expected to share in the possession of premaxillae and maxillae. In addition, he comments that these identifications 'are not seriously contradicted by the criterion of morphological relations, for both the lip area and the lateral nasal tooth plate bite immediately outside the dentary'. What is more, these

Fig. 6. A. Anterior palatal view of *Dipnorhynchus sussmilchi* (ANU18815) showing the fused-in 'dermopalatines' and the boss formed from the anterior median bone, as well as the distance between the occlusal surfaces and the postnasal wall. *B, C.* Anterior and posterior views of a snout fragment from an undescribed dipnorhynchid from Wee Jasper, N.S.W. (ANU36519). Note the pores (1) associated with the main lateral line canal which is indicated by the arrow, and the irregular row of pores (2) in the position of the infraorbital canal, but which open directly into the tubes of the ethmoid capsule. *D.* An isolated palate of *Speonesydrion iani* (ANU35646) showing the fused-in 'dermopalatines' and the space where the anterior median bone has failed to ossify or has fallen out. Compare this with the specimen of *D. sussmilchi* figured by Thomson and Campbell (1971: fig. 72). Natural size.

identifications 'avoid the assumption that the lip area and lateral nasal tooth plates are new structures'.

As indicated above, the matter should be approached first using data derived from the dipnoans themselves. After all, a statement of dipnoan relationships may be seriously modified by an interpretation of the homologies of these bones *within* the Dipnoi. It is illogical to decide first what the broad relations of the Dipnoi are, thus restricting the options in any discussion of homologies within the Dipnoi especially as these homologies are then used to identify a choana which becomes a significant part of the argument supporting the initially-accepted statement of broad relations.

It has been known for years that primitive dipnoans had highly ossified snouts, which seemed to be formed of a single massive rostral structure. Posterior to this was a large number of small dermal bones. These features are well shown by *Dipnorhynchus*, and they also occur in *Speonesydrion*. Denison's discovery that in *Uranolophus* the small bones continue over the rim of the snout to the edge of the anterior palatal recess, showed that in the most ancient genus no paired marginal bones had yet formed. We have examined Denison's material and agree completely with his interpretation of both the snout and the anterior bones of the mandible, which shows similar small plates. There is no evidence that the plates result from cracking — several show finished edges. (Incidentally, this pattern of small bones is retained in some species until the Late Devonian). *Uranolophus* indicates to us that the Dipnoi separated from the stock that was ancestral to them and their nearest neighbours *before* the bilateral symmetry of the paired external dermal bones of the rostral capsule of osteichthyans became established. (For further discussion, see below). No dipnoan described up to the present time shows pairing of these bones, but rather a single continuous sheet of bone. The pairing referred to by Rosen *et al.* is merely the bilateral symmetry of a single fused entity, which developed long after the dipnoan line was established.

In the second place, these bones are not tooth-bearing in the normal sense. In some genera they carry crude irregular tuberosities which no doubt enabled the animal to grasp passive food more effectively than it could with smooth bone. However, in other genera, including the most primitive ones — *Uranolophus*, *Dipnorhynchus* and *Speonesydrion* — no such tuberosities are present. In the genera in which tuberosities occur, the front edge of the mandible passes close behind them on closure, producing a grasping or shearing action. In the more primitive genera such a relation had not developed. The tuberosities are best regarded as secondary, derived several times, and of no phylogenetic significance.

In the third place, the fact that they bite outside the lower jaw is strictly irrelevant for the identification of maxillae and premaxillae. If the marginal bones of the Dipnoi were derived independently within the group by the fusion of a number of small bones, precisely the same situation could occur. After all, marginal bones in the two jaws should have some occlusal relationship. What else would one expect if they were to form an efficient system? But Miles comments that the relationship is not simply between these bones and the lower jaw, but specifically with the 'dentary', making it necessary to argue for the existence of that bone. As indicated by Denison (1968: 378) a good case can be made for the view that the 'dentary' like the 'premaxilla' is the result of fusion of small bones, and this fusion must also have occurred *after* the dipnoan stock became isolated.

Fourth, the argument that the bones lie in front of the anterior palatal recess is difficult information to handle. The recess is a space of unknown function anterior to the palate, and found in a variety of primitive actinopterygians, crossopterygians and tetrapods. Being only a space, and lying in different relationships with the bones behind it, can we say that it is a homologous 'structure' in all these groups?

Finally, the argument that these bones are in series with more posterior dentigerous bones identified as maxillae is really only a statement that they believe that the subnasal ridges are parts of maxillae, a position that Rosen *et al.* make no attempt to justify.

We conclude that no sound argument has yet been proposed to support the view that the median part of the rostral capsule with its tuberosities is the homologue of the premaxillae in other vertebrates.

On the other hand, the presence of an unconfined anterior narial opening in all dipnoans, and the presence of numerous bones at the rostral margin in the primitive forms, suggests that their upper lips are formed of external dermal bones that have been reflexed to various degrees on to the ventral surface of the rostrum. In some long-headed genera, such as *Griphognathus*, this reflexed area is very extensive and bears tuberosities that are merely irregularities in the enamel-coated dentine covering a continuous unpaired rostral bone. If bones homologous with the premaxillae of tetrapods were ever present in dipnoans, they have been lost during this reflexing process. The rostral capsule was formed by the fusion of small bones that were all originally on the dorsal and anterior surfaces of the head, posterior to the margin of the mouth.

Anterior Median Bone

In *Chirodipterus* the bone considered by Miles to be a vomer is opposed by a single bone in the mandible. No articulated specimens of *Dipnorhynchus* are available, but it is clear that the dentary would occupy most of the anterior palatal recess, and the triangular median area on the mandible (the adsymphysial plate) would oppose the anterior ends of the joined 'dermopalatines'. Consequently, there is no possibility of a median palatal bone of the same type as in *Chirodipterus* lying in front of the 'dermopalatines' in *Dipnorhynchus*.

However, ANU 18815 shows the median anterior palatal boss to be composed of three sections. Two are on the anterior ends of the pterygoids, and the unpaired median one is semi-isolated from them. The interpretation of this single boss has been difficult. Does it result from the inwards growth of the 'dermopalatines'? If so, why is it unpaired? Is it an isolated element? Another dipnorhynchid from Wee Jasper (ANU36508) has a space from which the median bone appears to be broken out cleanly, suggesting that it was a single element. The position is complicated by the presence of a natural gap in this position in one specimen of *D. sussmilchi* BMP33699, and in the only known palate of *Speonesydron*. These gaps could be best explained by the failure of a median element to ossify rather than by the failure of the well-developed 'dermopalatines' to occupy the space.

If it is agreed that a single median bone is present in these primitive forms, a new explanation for the median bone in *Chirodipterus* becomes possible. As the 'dermopalatines' retreated in the manner suggested below, the median element came to lie at the front edge of the palate. This process would be accompanied by the gradual isolation of the median 'adsymphysial plate' in the lower jaw. During subsequent evolution, these median plates in both the palate and the mandible have been lost.

This solution to the problem of the median plate has interesting consequences. (a) It explains why the bone is single. Miles in regarding it as a vomer had to explain why the vomers had fused. (b) It offers an adequate explanation of why the isolated adsymphysial plate of the mandible appears and then disappears during evolution. No explanation of this has previously been produced. (c) It accounts for the absence of a median plate in genera such as *Uranolophus* and *Griphognathus*. Other workers have had to assume that the plate had been present, but was not preserved.

We suggest that this bone is unique to dipnoans and that it is present only in

Devonian genera. We have no evidence that it was ever present in the denticulated palate line — certainly there is no evidence of its existence in *Uranolophus* in which the 'dermopalatines' meet the pterygoids apparently without an intervening median bone. However, the sutures between the parasphenoid and the pterygoids in the denticulated types are usually very difficult to observe, and we cannot be sure that the bone under discussion is absent. It will be obvious that we are not suggesting that this bone is the homologue of the bones referred to as vomers in *Neoceratodus* by most workers.

We will refer to this element informally as the *Anterior Median Bone*, preferring to do this rather than provide a new formal name.

Anterior Paired Palatal Bones as Dermopalatines or Vomers

As indicated above, these bones are represented by single paired elements in the primitive genera *Uranolophus*, *Dipnorhynchus* and *Speonesydrion*, in all of which they are sutured against or fused with the 'pterygoids', meet in the mid-line anteriorly, extend back to the postnasal wall, and flank the posterior naris.

Among later Devonian genera with tooth plates, paired bones in a similar position are known with certainty only in *Chirodipterus*. However, in that genus they are smaller than in the primitives, do not meet in the mid-line, and have become quite free of the 'pterygoids'. Although paired plates that may be homologues have been reported from other Devonian and Carboniferous genera (see Miles, 1977: 174), they are not preserved in position. In the early genera these paired plates are opposed by the anterior parts of the 'prearticular' tooth plates which extend well forward into the arch of the 'dentary'. In *Chirodipterus* the edges of the 'pterygoid' and 'prearticular' tooth plates match precisely. The 'dermopalatines' do not take part in the bite, and consequently they are in process of reduction. In later genera such as *Sagenodus* both upper and lower tooth plates become smaller and more sharply defined, with marginal addition of cusps taking place at a level well outside the occlusal surface (Smith, 1979). Clearly the 'prearticular' dentition was not in contact even with the margins of the 'pterygoid' dentition, and so functional 'dermopalatines' were not possible. It is reasonable to conclude that the trend to reduction seen in *Chirodipterus* was continued in later forms, and that the 'dermopalatines' were lost.

Among Devonian non-tooth-plated genera, paired anterior palatal bones are known in *Uranolophus*, *Griphognathus*, *Fleurantia*, and possibly *Holodipterus*. Insufficient detail is available to corroborate their presence in the post-Devonian *Uronemus*, but they seem to be retained in *Conchopoma*. The bones considered by Schultze (1975: fig. 5) to be vomers in *Conchopoma gadiforme*, lie at the front end of the pterygoids and the expanded parasphenoid, and must be adjacent to the posterior naris. We conclude that in this line they are retained because they provide a surface against which the broad flat basibrachial tooth plate can function.

The question of the homologues of these bones must now be considered. Miles considered them to be dermopalatines because he inferred that they lay against the pterygoids and behind the vomers (or vomer). This argument does not hold if the so-called 'vomer', in the primitive forms in which it is known, originated behind rather than in front of them. In any case, the palatines in primitive tetrapods lie well away from the mid-line and are commonly behind the choana. Topographically it is difficult to argue for this homology. Rosen *et al.* consider these bones to be vomers. They ignore the existence of the median bone in *Chirodipterus* and this enables them to avoid one significant difficulty in making the broad general comparison that is the basis of their determination. The pattern alluded to, however, depends also on the regularity of occurrence of the bone behind their 'vomer' — the one they refer to as the 'palatine' (Rosen *et al.*, 1981: fig. 7). We have shown that this bone is irregularly present in *G. whitei* and probably is only an individual variation. Consequently, the general pattern

argument fails and it is necessary to develop other criteria for the establishment of the homology of the bone.

Denticulated Bones on the Labial Lamina, Tectum Nasi and Postnasal Wall — are they Ectopterygoids, Lateral Nasal Tooth Plates or Maxillae?

Rosen *et al.* (1981: 186) interpreted these bones as maxillae because their denticles bite outside the lower jaw, and 'in no known gnathostome do palatal teeth bite outside the lower jaw'. This argument assumes that if teeth are not 'palatal' (without defining what is meant by that term) then they must be either maxillary or premaxillary. Another possibility, of course, is that they are associated with neither the normal palatal bones nor the normal marginal bones, but are secondarily developed for some new function. Moreover, these bones do not form part of the external dermal series, as they should if they are maxillaries. As shown above, the anterior bones lie on an endoskeletal ridge against the *inner* edge of the labial lamina (which is of endocranial origin) and form a lining on the neurocranial tissue lateral to the nasal capsule, whereas the posterior bones lie directly on the postnasal bar and extend forwards on to the labial lamina. All along their lateral edges they are well separated from the external dermal bone. These relationships would be entirely unexpected for a maxilla.

The difficulty of maintaining the distinction between 'palatal' and 'marginal' bones implied by Rosen *et al.* in the above quotation, is emphasized by the fact that their maxilla is interpreted by Miles (1977: 163) as an ectopterygoid. Though the reason for this homology is not explicit, it presumably is simply that Miles sees the bone as lying in series behind the dermopalatine, and lateral to the entopterygoid against which it is sutured. Again it is an overall pattern of bones that is being interpreted, and the pattern one sees depends on the model being used for comparison.

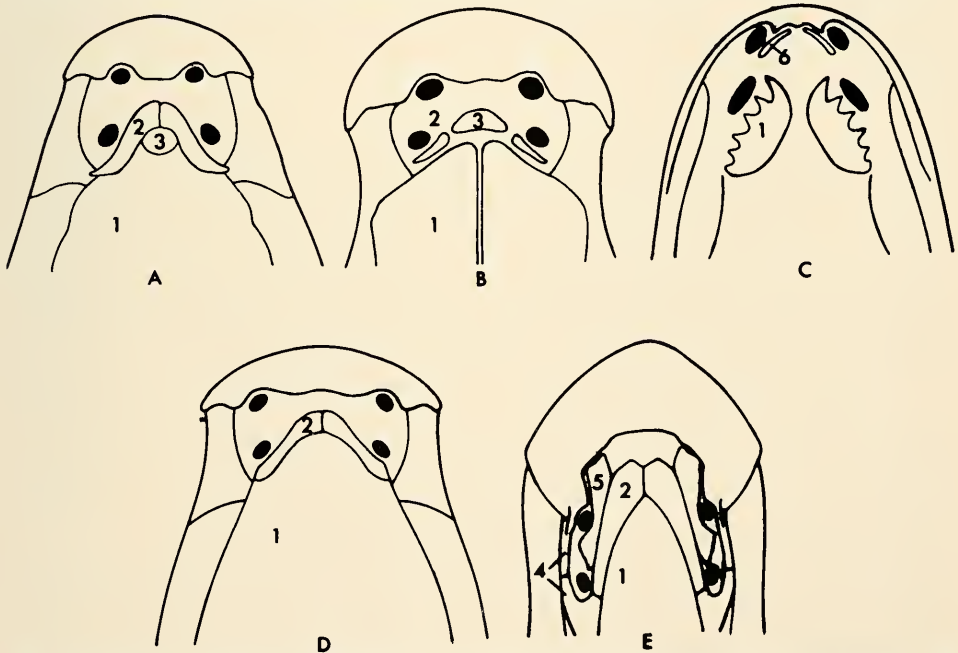


Fig. 7. Diagram showing plate homologies at the anterior end of the palate in (A) *Dipnorhynchus*, (B) *Chirodipterus*, (C) *Neoceratodus*, (D) *Uranolophus* and (E) *Griphognathus*. The bone names in quotes are not to be considered as homologues of bones of the same name in tetrapods. 1 = 'pterygoid', 2 = 'dermopalatine', 3 = anterior median bone, 4 = lateral nasal tooth plates, 5 = extra dermal bone, 6 = isolated lip bone. Nares black. Each diagram is the same width across the posterior nares.

As has been shown in the section dealing with occlusion, the elongation and depression of the snout, in association with the distinctive mode of feeding, results in the lower jaw coming into contact with the postnasal bar, and the lateral and ventral walls of the nasal capsule. These surfaces not only require protection, but they also form a significant part of the biting surface. The 'dentary' shears past the lateral nasal tooth plates, and the tusks on the 'prearticular' meet the denticles on the postnasal bar. Such an arrangement is not possible in highly arched forms whether they are of the tooth-plated or denticulated types. The postnasal bars of *Chirodipterus*, *Dipnorhynchus* and *Uranolophus* were situated some distance dorsal to the occlusal surfaces and were embedded in soft tissue (Figs 4A, 6A; Denison, 1968: fig. 9A). Moreover, the junction of the postnasal bar in *Uranolophus* with the subnasal ridge shows that no labial lamina was present and therefore there would be no lateral nasal tooth plates of the kind seen in *Griphognathus*. If other toothplates were present on the inner face of the postnasal ridge, they have not been preserved. Some denticulated plates are known in *Holodipterus*, but their relationships are unknown (Miles, 1977: 168, fig. 72). They are not necessarily precise homologues of those in *Griphognathus*.

We conclude that the maxillae (excluding the subnasal ridges) of Rosen *et al.* (1981), and the ectopterygoids and lateral nasal tooth plates of Miles (1977), are neomorphic in long headed dipnoans, *Griphognathus* being the only genus in which they are well known.

'Dermopalatine 3' or 'Extra Dermal Bone'

This bone meets the crest of the 'dentary', serving to form part of the bite, and to protect the ventral face of the nasal capsule and the anterior naris. It is also a neomorphic structure in this group. This view is implicitly supported by the work of Miles and Rosen *et al.*, because 'dermopalatines' are not known in this position in any other group, and the term 'extra dermal bone' is an acknowledgement that it has no homologue in other groups.

Summary

Jarvik (1972) and Bjerring (1977), depending mainly on embryological evidence, have also offered an independent interpretation of the bone homologies of the palate. This work is briefly summarized by Jarvik (1980: 397-404), and it is unnecessary to consider most of the detail here. The essential points are: (a) The homologies of the 'vomeres' in forms such as *Uranolophus* and *Neoceratodus* are questioned, those of *Uranolophus* being regarded as 'vestiges of the external exoskeleton of the snout which secondarily has been displaced inward into the mouth cavity', and that of *Neoceratodus* being 'formed by horizontal epal dental plates' of the terminal gill arch (Jarvik, 1980: 402-403). (b) The exoskeleton of the snout that has migrated into the mouth cavity has been 'partly retained in Devonian dipnoans and has disintegrated into a great number of exoskeletal elements. These elements, the subnasal plates, discovered by Miles (1977) and by him referred to as tooth plates or interpreted as ectopterygoids and dermopalatines were all situated in the mucous membrane in the roof of the mouth underneath the nasal cavities. To this category belong also the "lateral nasal plates" which were interpreted as vestiges of the maxillary' (Jarvik, 1980: 430).

We agree that the homology of the 'vomeres' has not been established by previous workers, and it will be apparent that we disagree with Jarvik and Bjerring on this point, though we have no comment on the embryological approach as such. We also disagree with the view that the so-called 'subnasal plates' are remnants of the external dermal bones, because they seem to appear only late in dipnoan history associated with the derived flat-snouted types. It is preferable to regard them as new structures developed in the skin below the nasal sacs to serve protective and grasping functions.

The paired anterior tooth-bearing plates in *Neoceratodus*, commonly referred to as

vomerine tooth plates, remain a problem. Unlike the paired plates in such forms as *Chirodipterus* (the 'dermopalatines') which lie behind the posterior nares, these plates lie mesial to the anterior end of the nasal capsules, and posteromesial to the anterior nares. Topographically it is difficult to argue a case for the homology of these 'vomerine tooth plates' and the 'dermopalatines' of *Chirodipterus*. It is also impossible to make a convincing argument for homologizing them with the 'anterior median bone' of *Chirodipterus*. Another possibility which is suggested by their position, by the fact that the upper lip turns back into the buccal cavity, and by the lack of ossification of the rostral region in post-Devonian dipnoans, is that these 'vomerine tooth plates' are the remnants of the median part of the upper lip — the so-called premaxillary of Miles and Rosen *et al.* The embryological work of Kemp supports this view. Her illustration of stage V in the developmental series (Kemp, 1977: pl. 4A) shows the vomerine tooth plates erupting just behind the fold of epithelium running between the anterior nares — that is, along the edge of the soft lip.

A summary of the inferred homologies of the various elements in the genera under discussion is given in Fig. 8.

BUT IS IT PARSIMONIOUS?

In suggesting that the anterior part of the palate of *G. whitei* contains several bones neomorphic in long-headed dipnoans, and that other bones such as the 'vomer' in *C. australis* cannot be homologized with bones in similar positions in other osteichthyans and tetrapods, we will be accused of having failed to use parsimonious argument. We reiterate, however, that parsimony is not a mode of argument to be used in the development of hypotheses about homology. If parsimony has any value at all in such discussions, it is only as a device for deciding between two or more hypotheses derived on other grounds, if analysis shows that these hypotheses have equal explanatory merits (Campbell and Barwick, 1982: 520). In such instances it may be preferable to choose the hypothesis that requires the least number of assumptions, but such a choice confers no special value on the hypothesis. It merely becomes the first basis for further work.

We have examined the relationships of cranial bones within the Dipnoi, taking into account a) the evolution of structures during the Devonian, b) the functional relationships of the bones around the anterior end of the palate and those in the lower jaw, as well as the tooth plates and other food reduction mechanisms, and c) the precise relationships of the bones in question to one another, to the neurocranium and to the nasal capsule. This examination leads to the conclusion that certain bones marginal to the buccal cavity in Devonian dipnoans were not in that position in their ancestors, and that other bones are neomorphic. In other words, account has been taken of evidence from morphology, function and sequence to reach conclusions about homologies.

The alternative hypotheses take no account of the level of evolutionary advancement of the animal — they take *G. whitei* to be primitive in the number and arrangement of the anterior palatal bones when it is acknowledged to be advanced in most of its other skull characters, and there is no supporting evidence of the presence of such bones in the genera generally acknowledged to be primitive. Nor do they consider the possibility of special structural requirements for the function of such an aberrant organism as *Griphognathus whitei*. Instead, they depend on the supposed recognition of similar patterns in this animal (taken as a representative primitive dipnoan), and other osteichthyans and tetrapods. That such an approach has led Miles and Rosen *et al.* to such disparate results, without any means of deciding which is correct, shows that pattern recognition of itself does not provide an adequate approach. To claim that their methods are more parsimonious than, and therefore preferable to, one requiring the postulation of neomorphic structures, even though the latter embraces more wide-

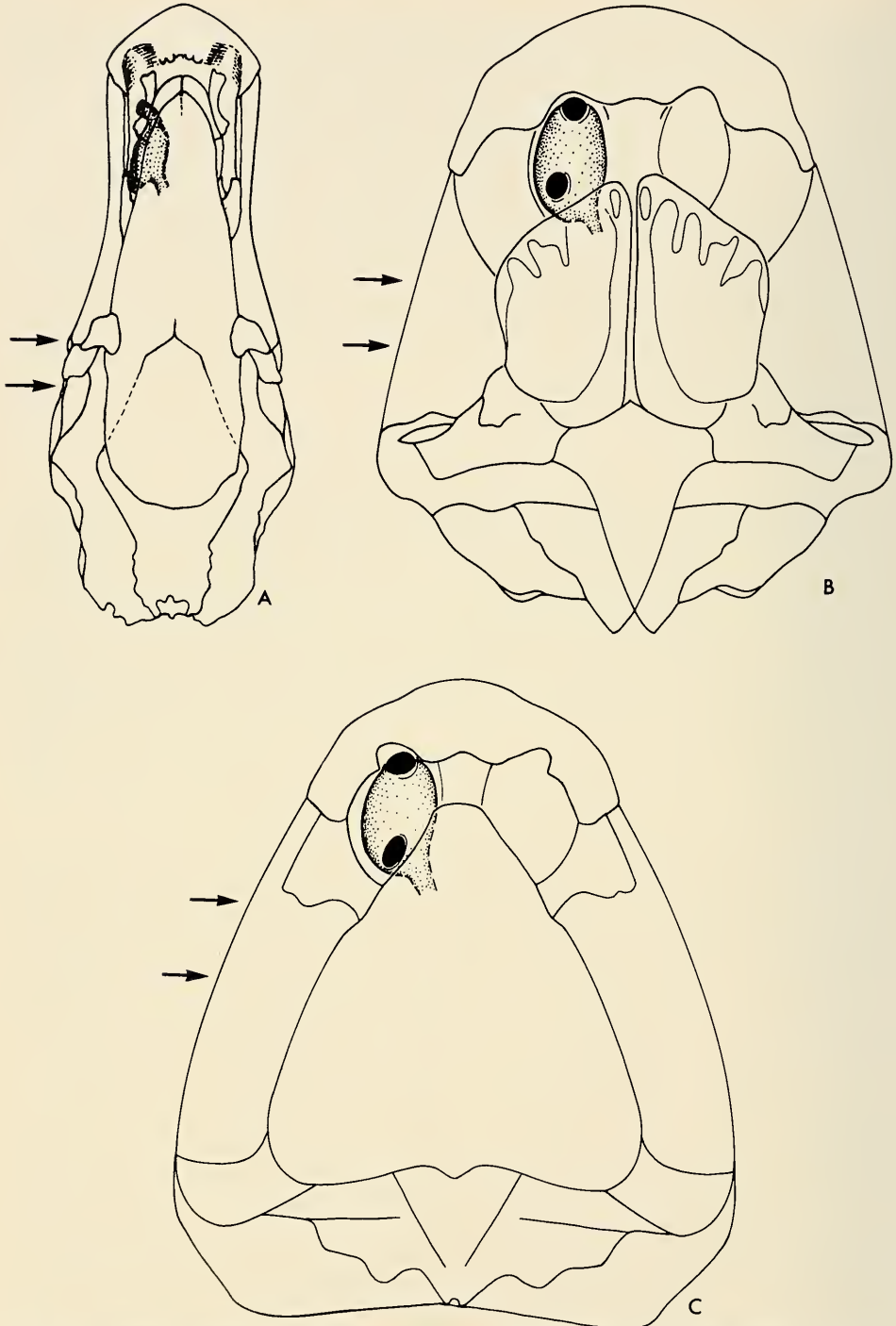


Fig. 8. Comparative diagram of (A) *Griphognathus*, (B) *Chirodipterus* and (C) *Dipnorhynchus* to show the position and size of the nasal capsule relative to the palate and the orbits. Positions of anterior and posterior nares (in black) are inferred from the structure of the surrounding bones, but we have no control on their shapes. Position of orbit indicated by arrows. Skulls reduced to the same length.

ranging data including the bone pattern and its origin and function, as well as the palaeoecological and stratigraphic evidence available from Devonian rocks, is simply irrelevant.

CONCLUSIONS

1. The attempt by Rosen *et al.* to establish the existence of a choana in *Griphognathus whitei* by homologizing bones around the posterior nasal opening with the palatine, maxilla and vomer of tetrapods, fails.
2. Several neomorphic bones are present around the anterior part of the palate of *G. whitei*. These are formed in long-headed dipnoans in response to a derived mode of feeding which is also reflected in the elongated depressed snout.
3. The so-called 'vomer' in *Chirodiptherus australis* is an unpaired median bone derived from an element that originally lay behind the paired 'dermopalatine' elements in *Dipnorhynchus* and *Speonesydrium*.
4. The identification of 'vomeres' and 'palatines' in dipnoans at all evolutionary stages is called in question.
5. Functional study of the nasal openings in living and fossil dipnoans indicates that they are incurrent and excurrent nares that have migrated into the mouth in response to the loss of marginal bones.
6. The attempt to homologize bones by matching their patterns with patterns in other groups, and then using the inferred homologies as evidence of taxonomic relationships between the groups, is obviously flawed.
7. Comparison of patterns within a group without an understanding of the functional significance and evolutionary origin of the patterns, inevitably produces spurious results. Pattern and process must be examined together.
8. Only after ingroup relationships are established is it safe to attempt an analysis of outgroup relationships.

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